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United States
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Forest Service

**Intermountain
Forest and Range
Experiment Station**

Research Note
INT-306

April 1981

# Differential Defoliation of Neighboring Douglas-fir Trees by Western Spruce Budworm

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# Differential Defoliation of Neighboring Douglas-fir Trees by Western Spruce Budworm

**G. I. McDonald**[1]

## ABSTRACT

*Color photographs document phenotypic variation of inland Douglas-fir populations in response to attack by western spruce budworm. Host-insect literature was reviewed and tentative hypotheses to explain the nondefoliated trees are suggested. The implications these various possible explanations have on future breeding programs are discussed.*

KEYWORDS: budworm resistance, *Pseudotsuga menziesii, Choristoneura occidentalis,* insect resistance progeny tests

Little is known of the host-pest genetic interactions in an ecosystem sense, but some sort of resistance-susceptibility, virulence-avirulence (or preference-nonpreference) polymorphology is known for every system that has been studied, such as chestnut blight caused by *Endothia parasitica* (Van Alfen and others 1975), stem rust of wheat caused by *Puccinia graminis* (Browning 1975), codling moth (*Laspeynesia pomonella*) on pears and apples (Westgard and others 1976), nymphaline butterfly (*Euphydryas editha*) on various host plants (Singer 1971), bluegrass billbug (*Spenophorus paroulus*) on bluegrass (*Poa pratensis*) (Kindler and Kinbacher 1975), and fusiform rust (*Cronartium fusiforme*) on southern pine (Snow and others 1976). Many more systems exhibit the more easily discerned polymorphology of variation in the host; for example, white pine blister rust caused by *Cornartium ribicola* (Bingham and others 1971); Douglas-fir needle cast caused by *Rhabdocline pseudotsugae* (Brandt 1960); *Lecanastecta* spp. causing needle cast on western white pine (Hoff and McDonald 1978). Also, Douglas-fir (*Pseudotsuga menziesii*) shows a polymorphic population in response to feeding damage by hare and deer (Dimock and other 1976).

Long-term host:pest interaction leads to a coevolved genetically interdependent system (Anikster and Wahl 1979; Harlan 1976; Price 1977). The degree of interdependence depends on time, environment through which time operated, current environment, and the genetic configurations of both host and pest at the beginning. Current theory indicates that the interdependent host-pest systems should be maintained because of the likelihood of drastic reduction of the host if only the host side is tampered with (Price 1977).

Consequently, the first step in any pest control effort should be to determine how much input natural forces, including genetic variation of host and pest, can make to the overall pest management effort (Kogan 1975). Costs skyrocket when control strategies ignore or defy these forces. The white pine blister-rust antibiotic spray program and *Ribes* eradication in the West are examples (Ketcham and others 1968). Much evidence generated in the development of control strategies for pests (including insects) of agricultural crops shows that a factor of prime importance to integrated control programs is the genetic interaction between the host population and the pest population (Tummala and Haynes 1977). Thus, regardless of the control strategy ultimately selected to deal with the western spruce budworm (*Choristoneura occidentalis*), a basic piece of information is the role host resistance plays in the interaction between budworm and its hosts.

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The initial genetic question is: Does phenotypic variation of the desired trait exist? Because genetic theory holds that phenotypic variation is composed of two parts—variation due to environment and variation due to genes—the following implication can be formulated: If Douglas-fir populations possess inherited resistance to western spruce budworm, then phenotypic variation in amount of damage after similar exposures to western spruce budworm should be observable in trees growing in the same environment. If no phenotypic variation is readily observed, then inherited traits will be difficult to detect. So, existence of phenotypic variation would signify the possible existence of a genetic component in the Douglas-fir, western spruce budworm interaction.

## Phenotypic Variation of Spruce and Balsam Fir

Most information available deals with white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*) damaged by the eastern spruce budworm (*Choristoneura fumiferana*), in eastern Canada. Typically, 90 to 97 percent of the merchantable balsam fir is destroyed during an outbreak that runs its full course (Blais 1954; Ghent 1958). On the other hand, few understory seedlings of balsam fir are killed (Ghent 1958).

During an outbreak, white spruce intermingled with balsam fir is much less subject to mortality (Ghent and others 1957) than the balsam fir. Specific estimates of white spruce mortality were not found, but there is a striking difference in mortality levels between white spruce and balsam fir. More information is needed in order to determine why white spruce is more resistant than balsam fir.

Comparison of radial growth patterns between host and nonhost trees growing in eastern Canada (Blais 1954, 1965, 1968) demonstrates that many white spruce and an occasional balsam fir can survive repeated budworm outbreaks. At one location in Quebec, six white spruce were found that had each survived six outbreaks over the last 300 years. Blais does not state how many balsam fir were included, but apparently several around 125 years of age were found. These balsam fir trees survived two outbreaks between 1835 and 1960. Specific references to resistance in these species to eastern spruce budworm have not been found, but survival of individuals through repeated outbreaks argues for their possession of phenotypic resistance.

## Phenotypic Variation of Douglas-fir

Many Douglas-fir growing in the Montana Rocky Mountains survive severe budworm outbreaks (Johnson and Denton 1975). Also, 1-year-old Douglas-fir seedlings showed a significant amount of stand related variation in degree of defoliation after exposure to field-collected third and fourth instar *C. occidentalis* larvae (McDonald 1979). Because references are not available, we conducted a search for cases of differential defoliation and survivorship in outbreaks of western spruce budworm in Douglas-fir stands of Montana and Idaho.

The purpose of this paper is to document the results of this search and interpret the findings in preparation for future progeny tests and breeding programs.

## METHODS

We searched for stands of Douglas-fir that have withstood budworm outbreaks or are currently being severely defoliated. Side-by-side cases of dead-living and defoliated-undefoliated trees were photographed. Each member of a photographed pair was required to be about the same size, have their branches intertwined, and their roots growing in similar soil. We attempted to obtain pairs located at several different locations to survey a variety of outbreak conditions and stand ages. For this initial survey, data consisted of photographs of pairs and some closeup comparisons of branches. An analysis of radial growth data will be the subject of another report. Phenotypic variation was documented in the following stands:

Lolo National Forest:
  Cedar Creek—lower R. 26 W., T. 16 N., S. 22; upper R. 27 W., T. 15 N., S. 8 and 9; middle R. 27 W., T. 16 N., S. 33.
  Camel's Hump—R. 28 W., T. 19 N., S. 32.
  South Fork, Little Joe Creek—R. 30 W., T. 17 N., S. 5.
Helena National Forest:
  Sheriff Gulch—R. 1 E., T. 11 N., S. 3.
Lewis and Clark National Forest:
  Spring Creek—R. 10 E., T. 10 N., S. 11.
  Green Mountain—R. 7 E., T. 11 N., S. 3.
Payette National Forest:
  Goose Creek—R. 2 E., T. 19 N., S. 15.
Salmon National Forest:
  Hull Creek—R. 20 W., T. 25 N., S. 24.
  Panther Creek—R. 21 W., T. 21 N., S. 33.

## RESULTS

At Spring Creek on the Lewis and Clark National Forest near White Sulfur Springs, Mont., there are clearly several survivors of an intense epidemic (fig. 1, photographed in July 1975 about 10 years after the outbreak collapsed). In 1978 these survivors were still under attack but they were growing well. Much regeneration about 10 years old was also evident under the survivors (fig. 2).

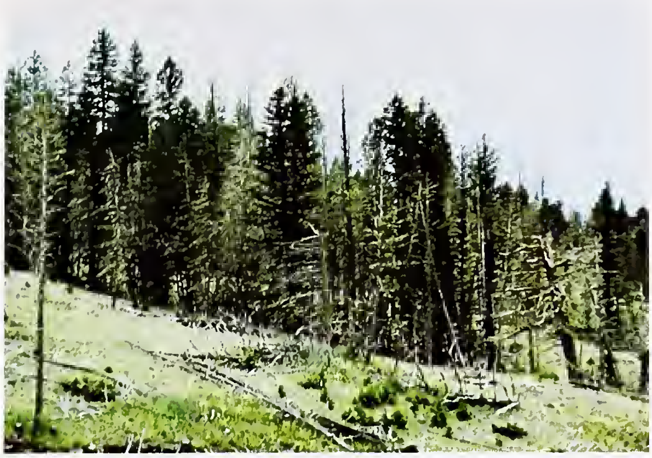

*Figure 1.—Douglas-fir trees 150 to 200 years old that survived intense epidemic of mid-1960's. Spring Creek drainage on the Lewis and Clark National Forest. Photo taken July 1975.*

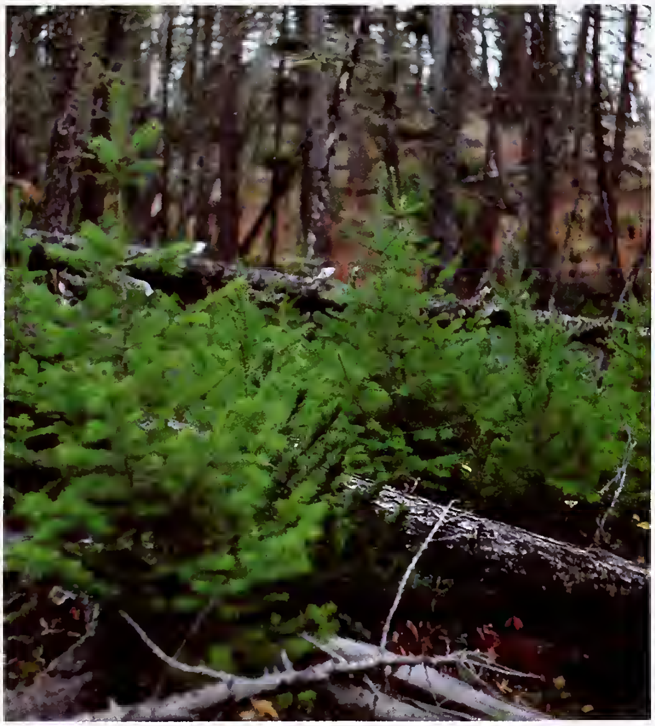

*Figure 2.—Douglas-fir reproduction in the Spring Creek stand. Photo taken in October 1977.*

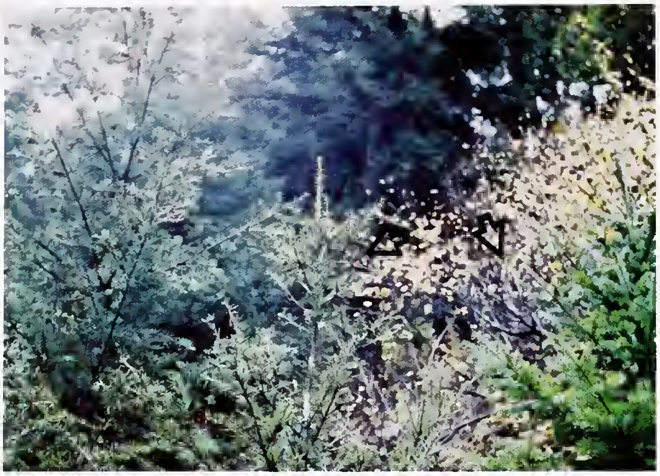

*Figure 3.—Differential defoliation of Douglas-fir reproduction in the South Fork of Little Joe Creek drainage on the Lolo National Forest during a budworm outbreak. Photo taken in early October 1977.*

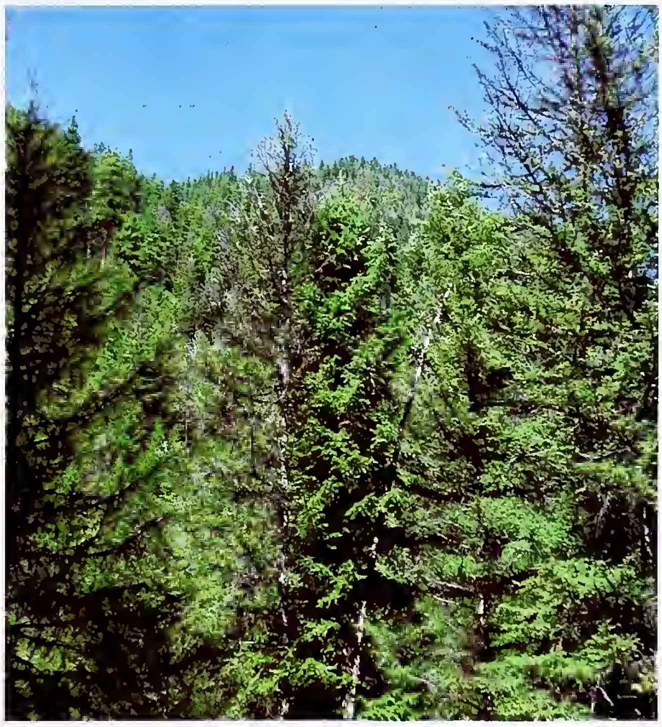

*Figure 4.—Differential defoliation of Douglas-fir stems during an outbreak in the Cedar Creek drainage on the Lolo National Forest. Notice undefoliated crown at photo center entwined with defoliated corwn. Photo taken in early September 1978.*

On the South Fork of Little Joe Creek on the Lolo National Forest near St. Regis, Mont., in early October 1977, we observed striking differential defoliation of Douglas-fir reproduction about 8 to 10 ft (2.4 to 3 m) in height. As seen in figure 3, the tree on the right edge of the photo was evidently much less severely defoliated than the trees on the left and in the middle.

In early September 1978, we observed a stand located in the Cedar Creek drainage on the Lolo National Forest near Superior, Mont. In figure 4, four levels of defoliation that vary from nearly complete (tree to the immediate left of the full-crown tree) to almost no defoliation are evident. In figure 5, four defoliated and two nondefoliated crowns are clearly visible. Many of the nondefoliated crowns were producing cones in 1978 even though the epidemic did not collapse until the summer of 1978.

Another differential reaction was recorded from the Camel's Hump area near St. Regis in late June 1978. Field observations of several pairs of heavily defoliated and lightly defoliated Douglas-fir showed in each case very striking differences. The heavily defoliated trees all exhibited severe top kill, much bud kill, and foliage was

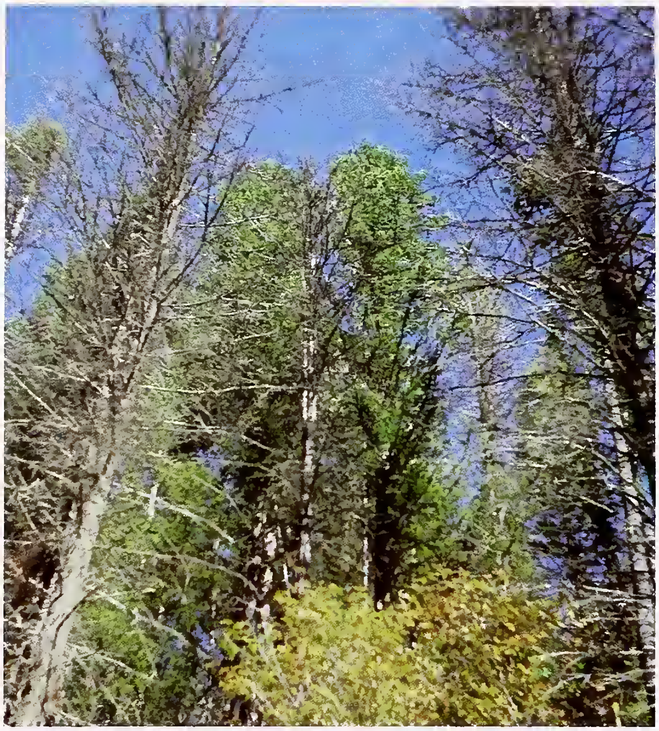

*Figure 5.—Differential defoliation of 75-100 year old seed-bearing Douglas-fir in the Cedar Creek drainage on the Lolo National Forest. Photo taken in early September 1978.*

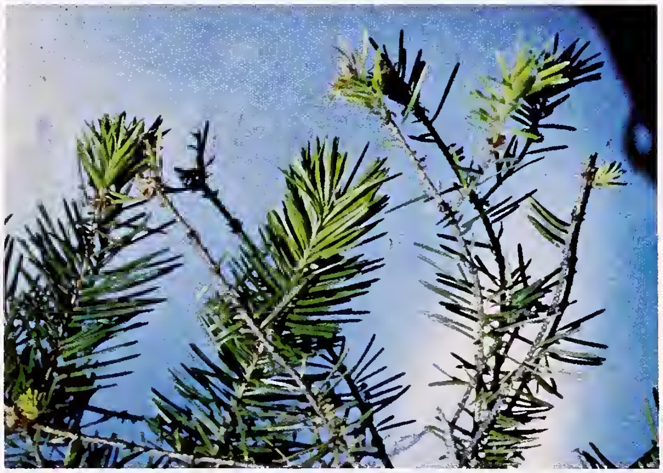

*Figure 6.—Close-up of defoliated branches from mid-crown of 75 to 100 ft tall Douglas-fir growing on Camel's Hump near St. Regis, Mont. Two branches on left from "green crown" and three branches on right from "gray crown." Photo taken in late June 1978.*

largely limited to the current year's needles. Many budworms were evident on both nondefoliated and defoliated trees. Defoliation and budworm population estimates were made on sample branches taken from midcrown of trees 40 to 75 ft (12 to 22 m) tall. One comparison of defoliation on trees about 60 ft (18 m) tall is shown in figure 6. The green member of the pair (branches on the left) exhibited no evidence of top kill and few dead buds, 50 to 95 percent of the foliage remained on the last 6 years of branch wood, and even though this tree contained a much larger number of feeding sites (branch tips) it supported an estimated 60 to 90 percent fewer larvae than the crowns represented by the branch on the right.

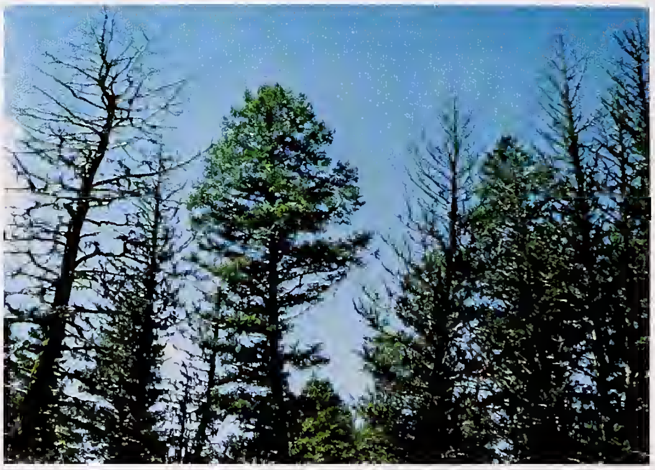

*Figure 7.—Dead and "full crown" old growth Douglas-fir at Green Mountain, Lewis and Clark National Forest, about 10 years after collapse of outbreak. Photo taken July 1975.*

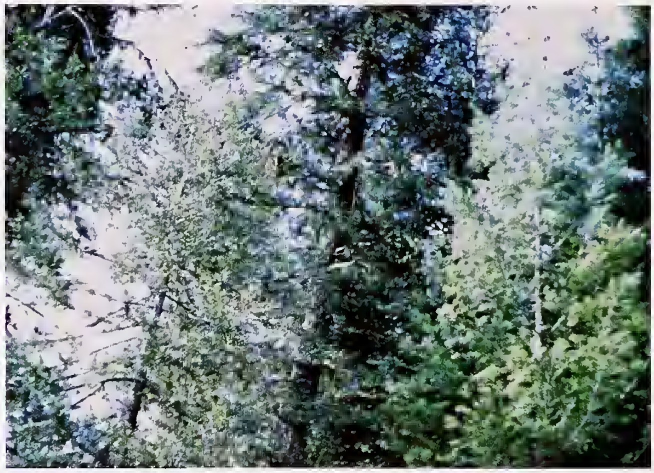

*Figure 8.—Comparison of grand fir (tree on left) and Douglas-fir (tree on right) defoliation. Goose Creek, Payette National Forest. Photo taken September 1978.*

In mid-july 1975, we visited a stand located on Green Mountain near White Sulfur Springs, Mont. Figure 7 shows a typical "full-crown" survivor of a severe outbreak that had collapsed about 10 years before. In early October 1977, we took branches from such crowns at Green Mountain for rooting studies and noted some current defoliation.

A stand of mixed grand fir (*Abies grandis*) and Douglas-fir growing on Goose Creek of the Payette National Forest was visited in early September 1978. This stand contained a young Douglas-fir (small tree on the right, fig. 8) with a complete crown and a young grand fir (small tree on the left, fig. 8) with severe defoliation. But directly across a dirt road about 50 ft (15 m) from the nondefoliated Douglas-fir was the crown shown in figure 9, a Douglas-fir that was almost completely defoliated.

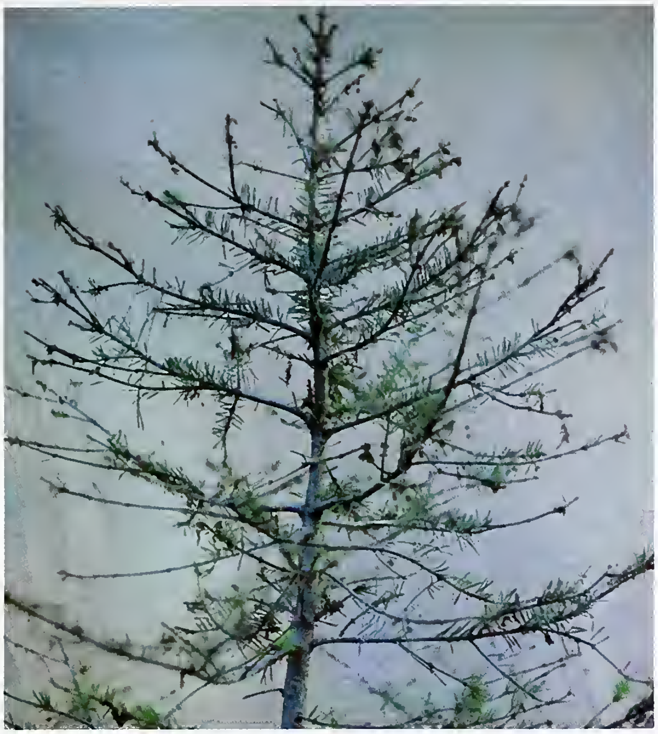

*Figure 9.—Heavy defoliation of a small Douglas-fir tree about 50 ft from the nondefoliated Douglas-fir shown in figure 8.*

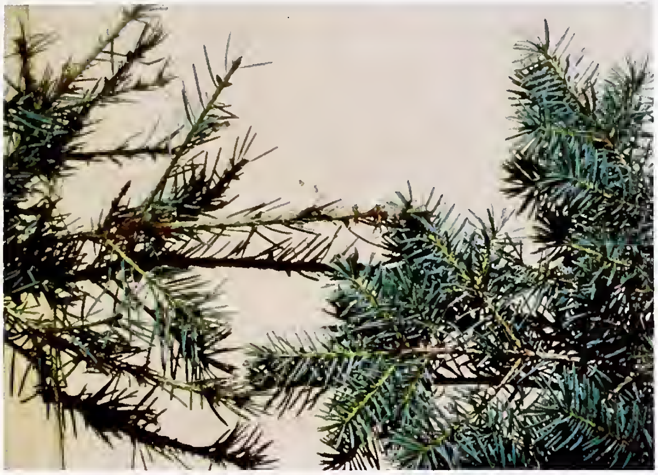

*Figure 10.—Close-up of mid-crown samples from adjacent Douglas-fir shown in figure 11 at end of first season's defoliation by western spruce budworm. Hull Creek, Salmon National Forest. Photo taken September 1978.*

A new outbreak of western spruce budworm was under way on the Salmon National Forest in 1978. We visited some of these stands in early September 1978. One case at Hull Creek shows very clear differential defoliation. The branches shown in figure 10 came from the same level in the crowns of the two forward trees in figure 11. The current foliage of the tree directly to the left of the arrow (fig. 11) was almost completely gone (branch on left of fig. 10) while the tree on the right shows almost no defoliation (branch on right of fig. 10). A comparison found at Panther Creek on the Salmon National Forest shows much the same thing

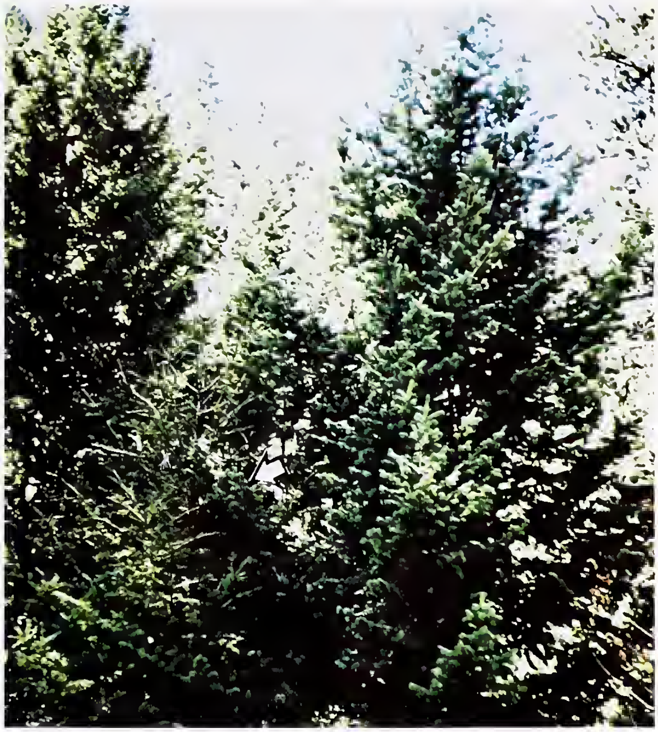

*Figure 11.—Intertwined crowns of defoliated and nondefoliated Douglas-fir (close-up in fig. 10) in the first year of an outbreak. Hull Creek, Salmon National Forest. Photo taken September 1978.*

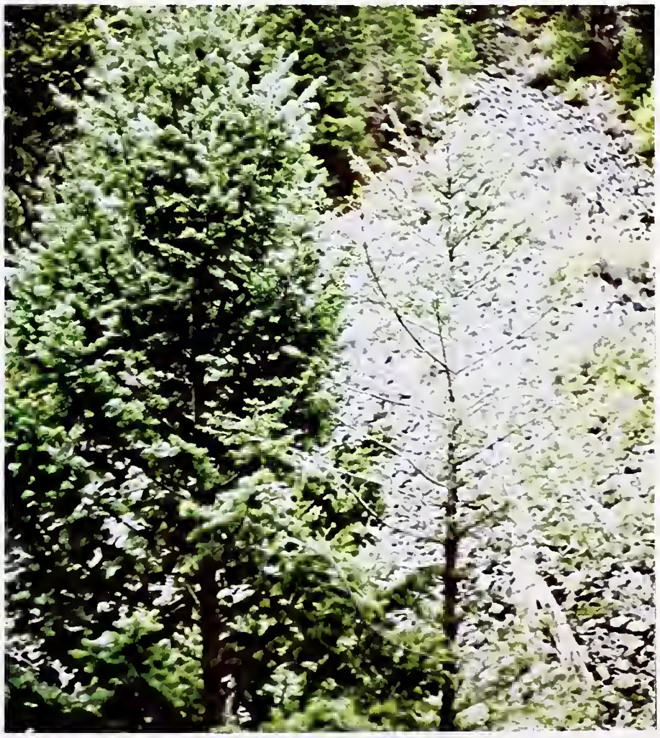

*Figure 12.—Nondefoliated and defoliated Douglas-fir in a chornic outbreak. Panther Creek, Salmon National Forest. Photo taken September 1978.*

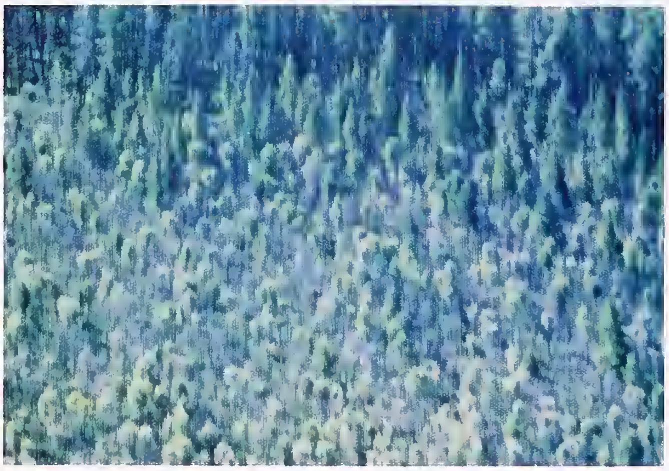

*Figure 13.—Green crowns after an intense outbreak in a densely stocked pure Douglas-fir stand. Sheriff Gulch, Helena National Forest. Photo taken July 1975.*

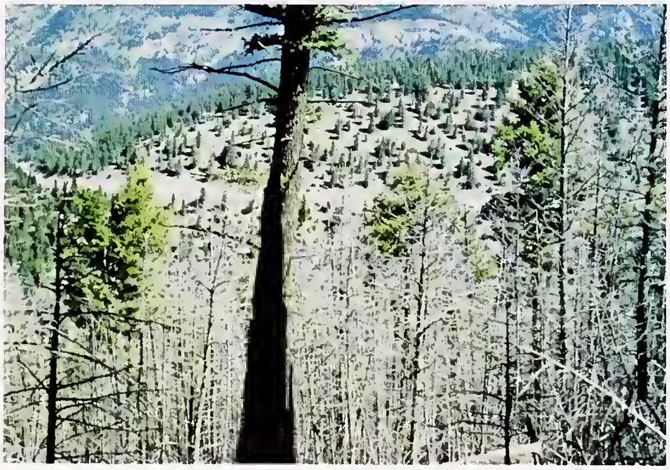

*Figure 14.—Close-up of the green crowns in figure 13. Notice the number of dead stems. Sheriff Gulch, Helena National Forest. Photo taken July 1975.*

except that this area apparently had a chronic infestation. The tree on the right in figure 12 has apparently been subjected to many years of repeated defoliation.

The last area to be discussed is Sheriff Gulch on the Helena National Forest. A telephoto photograph (fig. 13) shows the distribution of surviving crowns in a severe outbreak in relatively young Douglas-fir. The relatively high level of mortality in this stand is shown in figure 14. Rooting material was collected from this stand in early October 1977, and evidence of light to medium defoliation was observed in the surviving crowns.

## DISCUSSION

The defoliation polymorphism reported by Johnson and Denton (1975) seems to be widespread in Douglas-fir populations subjected to western spruce budworm defoliation. Does polymorphism indicate the existence of a potential budworm management option? The answer depends on the factors causing the condition and their amenability to management. The objective of this discussion is to examine possibilities and develop testable hypotheses that will explain the existence of "green" Douglas-fir. Propositions to be examined include moth escape; physiographic location; moth oviposition preference; hibernacular site selection of first instar larvae; larval feeding preference, including foliage toxicity; pheromone chemistry; parasite and predator effectivenes; and host-insect phenologic asynchrony. In the conclusion, we will discuss the impacts of the hypothesized relationships on a possible breeding program.

### Escape

The green trees could be the result of escape. I find it difficult to accept this explanation given time available and budworm numbers and behavior patterns during outbreaks. The most powerful argument against escape is that as the outbreak builds, the foliage of most trees is almost entirely consumed. Thus the green trees become a resource in ever increasing demand by a much increased population. Yet, they remain green.

### Physiographic Location

The undefoliated trees could be growing on a microsite that renders them less desirable to the budworm or more desirable to some budworm predators or parasites. We could not find any literature pertaining specifically to this proposition. Also, the current study was designed to minimize this possibility. The comparisons were made from the viewpoint of eliminating microsite variation. If the polymorphism cannot be explained satisfactorily by the other propositions, we would give this one more weight and accept the possibility that host-insect genetic interaction is not playing a role.

### Moth Oviposition Preference

The green trees may have resulted from receiving fewer eggs than their neighbors during an outbreak. Does *Choristoneura* exhibit oviposition preference? There are at least two mechanisms leading to oviposition preference. The first deals with directed host selection through use of the senses of sight and or smell. Female *Heliconius* butterflies are known to possess a complex system that utilizes both senses for oviposition-host selection from members of the family *Passifloraceae* (Benson and others 1974). A large literature has developed over the last few years that details many of the specific host-oviposition interactions as well as other plant-insect communications. Much of this knowledge was summarized by Kogan (1977) in his development of six classes of host-selection strategies. Since the budworms most likely fall into Kogan's class V where oviposition is selective, we can assume that a *Choristoneura* female actively selects hosts.

The second mechanism of host selection for oviposition is the passive process exemplified by oak winter moth (*Operopthera brumata*) (Feeny 1976) and other moths characterized by flightless females. In these situations, because of lack of mobility, the females are obliged to oviposite on their food genotype. *Choristoneura* seems to exhibit an intermediate response. Well-fed females probably lay most of their eggs on their food genotype, judging from the Sander and Lucuik (1975) findings about the effects of photoperiod and moth size on flight and oviposition behavior. More well-fed females laid eggs before they tried to fly than the starved insects. In fact, most starved insects flew before they oviposited. Thus, under conditions of low defoliation most eggs are probably laid on the female's food genotype, and under high defoliation most eggs would be laid after dispersion.

## Hibernacular Site Selection

*Choristoneura* spends the first 1 to 5 days after hatching searching for a suitable hibernation site (Harvey 1957). Wellington and Henson (1947) reported that *C. fumiferana* larvae crawled from the egg onto the needle and then moved toward the needle tip. If overcrowding occurred, many of the larvae would "drop" from the crowded needles. The question is whether or not the larvae "drop" directly from the egg. Do first instar larvae communicate with the tree on which they hatch? There is some evidence that oak leaf roller females can "imprint" their eggs with a chemical message to their larvae to exhibit a feeding preference for the female's food genotype (Hendry and others 1976). Such an imprint could be passed to first instar larvae so that the larvae could decide whether to drop directly from an egg or to crawl onto the surface of the needle depending on whether or not the egg was located on the female's food genotype. Budworm larvae spin a thread at all times (Harvey 1957). Thus, some of their actions can be inferred from their "tracks." We observed threads hanging directly from hatched eggs of all three clusters on one 6-year-old Doulgas-fir (author's unpublished data). Does this mean that these larvae dropped without crawling? Conversly, we have observed newly hatched larvae crawling from eggs to needle surfaces when eggs were depositied on needle population composed of the female's food genotypes.

## Larval Feeding Preference

Upon completion of diapause requirements and onset of warmer spring weather, the hibernating larvae become active and start searching for feeding sites. They generally mine the previous year's needles, new vegetative buds, or developing floral parts. Much literature indicates various kinds of chemical messages may be involved in determination of insect feeding sites. Some of the possibilities are specific or general excitants and restricted or general deterrents (Kogan 1977). There is considerable current interest in the general and specific feeding deterrents (Rhoades and Cates 1976).

A different mechanism of specificity determination (Hendry and others 1976; Rodriguez and Levin 1976) involves the "imprinting" of eggs with a substance obtained by the female from the plant she fed on. Hendry and others (1976) reported that such a system may be operating in oak leaf roller populations. They show that larvae of oak leaf roller hatching from eggs laid on scarlet oak prefer to feed on scarlet oak. But in the early instars, they will feed on other species of oak. Last instar larvae reared on scarlet oak will not feed on other oak species. The larvae die rather than feed. When oak leaf roller larvae are forced to feed on black oak during early instars they will not change back to scarlet oak in the last instar.

In light of recent findings, a contribution by the male to any imprint must be considered a possibility (Boggs and Gilbert 1979). Male Lepidoptera were shown to supply nutrients to the female through the sperm and spermatophore. These nutrients found their way into both the female and her eggs. Some plant products are presumably passed to budworm eggs from the female because *C. fumiferana* reared on artificial diet lay blue eggs as opposed to the normal green eggs (McMorran 1965).

Another example of food selection concerns two moths of the family Tortricidae. They are believed to be general angiosperm feeders that also occasionally feed on conifer seedlings (Martin 1958). Both *Tortrix alleniana* (*Aphelia alleniana* according to McKay 1962) and *Tortrix pallorana* (*I. clemensiana, Spraganothis sulfurerna, Amelia apllorama*, and *Aphelia pallorama* according to McKay 1962) were observed to behave as follows. Eggs were laid almost exclusively on white sweet clover (*Melilotus alba*) and alfalfa (*Medicago setiva*). Upon hatching larvae dispersed to find feeding sites. If they found a site on either white sweet clover or alfalfa they remained there to pupation. On the other hand, if they began feeding on other herbaceous plants, they frequently found their way to various conifer seedlings. Feeding times on these conifers varied from short to extended. These observations can be interpreted to agree with the oak leaf roller hypothesis. No evidence was given as to the oviposition preference of the moths raised on nonpreferred hosts or on the food preference of the resulting larvae.

## Pheromone Chemistry

Before we discuss other possible explanations for the existence of green trees, we should look at the role of pheromones, since patterns of variations in pheromone chemistry coupled with differentiation of budworm populations on individual host plants could account for the observed defoliation patterns. Host plants apparently can play a significant role in the pheromone chemistry of some insects (Hendry and others 1976) and intraspecies host-mediated-differentiation of insect populations is a real possibility (Feeny 1976; Edmunds and Alstad 1978). European cornborer (*Ostninia nubilalis*) can produce at least three kinds of pheromone based on the proportion of Z and E isomers of 11-tetradecenyl acetate (Klun and Maini 1979). These pheromonal differences are expressed as genetically controlled traits that are characteristic of different populations of European cornborers. Corn var-

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